Morphological data show that *Hyla dayi* Günther, 1897 (Amphibia: Anura: Hylidae) should never have been assigned to *Nyctimystes*

Fred KRAUS

Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA. Email: fkraus@umich.edu.

Citation: Kraus, F. 2013 06 30. Morphological data show that *Hyla dayi* Günther, 1897 (Amphibia: Anura: Hylidae) should never have been assigned to *Nyctimystes*. *Memoirs of the Queensland Museum – Nature* 56(2): 581–587. Brisbane. ISSN 0079-8835. Accepted: 16 June 2012

ABSTRACT

The treefrog described as *Hyla dayi* Günther and now known as *Litoria dayi* is restricted to the Wet Tropics of northern Queensland and has long been a source of taxonomic confusion. For many years this species was placed in *Nyctimystes*, but here I show that this frog never met the morphological criteria for assignment to that genus, which has long been defined by the combination of a vertically oriented pupil and the presence of a reticulum of coloured lines on the palpebrum. In particular, this species lacks the diagnostic vertical pupil on the basis of which *Nyctimystes* was originally erected. This is important because recent molecular studies have used this species and its erroneous generic assignment to provide misleading phylogenetic "tests" purporting to refute the monophyly of *Nyctimystes*. Recognising that *L. dayi* was never properly placed within *Nyctimystes* obviates these claims. Morphological and more recent molecular evidence both support a monophyletic *Nyctimystes* restricted to the Papuan region. I note an additional cranial character that, upon broader taxonomic investigation, may further support the monophyly of that genus. ❐ Litoria dayi, Nyctimystes, *Pelodryadinae*, *Queensland*, *Treefrog*, *Wet Tropics*.

The pelodryadine hylid frog originally described by Günther (1897) as *Hyla dayi* and currently known as *Litoria dayi* is restricted to a small area of the northern Queensland Wet Tropics and has been the source of considerable taxonomic confusion, the ramifications of which continue to the present. The holotype is lost (Tyler, 1968) and the original description was not particularly detailed, and this led to confusion as to which frog species the name properly applied. Liem (1974), in a review of northern Queensland small-eared treefrogs, showed that Günther's name *H. dayi* was not properly assigned to the frog previously referred to as *Litoria dayi* by Loveridge (1935), Copland (1957), and Tyler (1968). He showed instead that the original description better accorded with frogs then placed in the genus *Nyctimystes*, but he could not clearly assign the name to any of the three Queensland *Nyctimystes* species then recognised. Liem (1974) then provided a name for the frog erroneously treated as *L. dayi* by Loveridge (1935), Copland (1957), and Tyler (1968), describing it as *L. nyakalensis*. It is this early assignment of *Hyla dayi* to *Nyctimystes* that continues to provide problems for modern taxonomy.

Frogs placed in *Nyctimystes* were first distinguished from all other Australo-Papuan hylids on the basis of having the long axis of the pupil oriented vertically instead of horizontally. Boulenger (1882) erected the genus *Nyctimantis* for an Ecuadorian hylid having a vertical pupil and then later assigned new treefrog species from New Guinea to that genus on the basis of sharing that same feature (Boulenger,

1897, 1914). Stejneger (1916) pointed out the improbability of frogs from those two continents being directly related phylogenetically, noted that the South American species had the skin co-ossified with the skull whereas the Papuan species did not, and provided the replacement name *Nyctimystes* for the Papuan species. That name was then used for additional Papuan species having a vertical pupil (Parker 1936). The first comprehensive review of *Nyctimystes* described seven additional species, transferred two species to and removed four species from the genus, and provided a re-definition that included more characters (Zweifel 1958). Since that time, *Nyctimystes* has been defined as having the unique combination of (1) the contracted pupil forming a vertical slit, (2) a reticulum of pigmented lines on the transparent membrane of the lower eyelid, (3) the tip of the first toe not reaching the disc of the second, and (4) the skin not co-ossified with the skull. The last two characters serve to distinguish *Nyctimystes* from unrelated American forms having a vertical pupil and/or palpebral reticulum, such as *Agalychnis* and *Nyctimantis* (Zweifel 1958), leaving the combined presence of a vertical pupil and a palpebral reticulum as the definitive character combination distinguishing *Nyctimystes* among the Australo-Papuan pelodryadine hylids.

Nyctimystes was first thought to be represented in Australia when Tyler (1964) described *N. hosmeri* and *N. vestigea*, each on the basis of a single specimen. He later (Tyler 1968) transferred *Hyla tympanocryptis* (Andersson 1916), also known only from the holotype, to *Nyctimystes*. These generic assignments were based on the presence in all examined specimens of the palpebral reticulum characteristic of *Nyctimystes*, but the second diagnostic feature – vertical orientation of the pupil – was left unremarked. As noted above, Liem (1974) later showed that frogs referable to *Hyla dayi* also belonged with these three presumptive *Nyctimystes* species. Czechura *et al.* (1987) examined 174 specimens of *Nyctimystes* from Queensland, including all extant type material, and showed that all four of these names apply to only one variable species, for which *Hyla dayi* (Günther 1897) was the oldest available name. Since that time, *Nyctimystes dayi* has been considered the sole Australian representative of the genus, which has two dozen additional species described from New Guinea and one known from Halmahera, Indonesia. On the basis of a phylogeny derived from DNA sequence data, Frost *et al.* (2006) synonymised *Nyctimystes* with *Litoria*; therefore, this frog is currently referred to as "*Litoria dayi*".

During a casual examination of specimens of *Litoria dayi* in the collection of the Australian Museum, Sydney, I noticed that some specimens clearly had the contracted pupil oriented horizontally instead of vertically. To assess the generality of this surprising finding, I later examined the much larger collection of specimens of the same species in the Queensland Museum to determine whether intraspecific variation occurred in this feature. I report my findings and their taxonomic implications here.

MATERIALS AND METHODS

I examined pupil shape and long-axis orientation in all 394 specimens of *Litoria dayi* in the collections of the Australian Museum, Sydney (AMS) and the Queensland Museum (QM). Examined specimens included topotypic material of all named forms, all but three specimens (the three extant holotypes) examined by Czechura *et al.* (1987), and 223 additional specimens collected since that study. I confirmed that specimens were correctly assigned to *L. dayi* by verifying the presence of the palpebral reticulum in each; *L. dayi* is the only Australian hylid to have this feature. Because of the large number of specimens involved, the brief duration of my visits, and the fact that my findings were uniform and unambiguous with respect to pupil morphology I did not record catalogue numbers for each specimen involving each of the three pupil states: widely dilated, contracted and horizontally oriented, or contracted and vertically oriented.

Material Examined. *Litoria dayi (n=394).* Australia: Queensland: Alexandra Creek, McDowall Range, 16° 6′ 45″ S, 145° 20′ 50″ E (QM J66037–38); Atherton, 17° 16′ S, 145° 29′ E (AMS R39722); Atherton Rd, just before Mt Hypipamee National Park, 17° 26′ 0″ S, 145° 29′ 0″ E (QM J29524–25); Atherton Tableland, 17° 16′ S, 145° 29′ E (QM J25080, J25084–85); Babinda Creek, Babinda, 17° 22′ S, 145° 55′ E (QM J55599–607, J55617–25, J55627, J56145–47); Barron River, 17° 3′ S, 145° 26′ E (QM J13012, J43620–23, J55842–43); Bartle Frere, 17° 27′ S, 145° 52′ E (QM J30914, J32072, J32093–94, J32099, J32113, J32119, J32124, J32133–34, J32170–72); Beatrice River, near Millaa Millaa, 17° 33′ S, 145° 39′ E (QM J54923–25, J55628–32, J56182–85, J56493–94, J56496–97); Behana Gorge, 17° 10′ S, 145° 49′ E (QM J61844); Big Tableland, 15° 42′ 30″ S, 145° 16′ 30″ E (QM J60914); Billy Creek, 17° 49′ 25″ S, 145° 47′ 5″ E (QM J48220–21); 16 km from Bloomfield River, 16° 2′ S, 145° 15′ E (QM J36324–25); Broadwater Creek National Park, 11 km S Mt McAlister, 18° 23′ 30″ S, 145° 56′ 30″ E (QM J61211–12); Bushy Creek, near Julatten, 16° 36′ S, 145° 20′ E (QM J55626); Cairns Intake, Lake Placid Station, 16° 52′ S, 145° 40′ E (QM J55580–82); Cape Tribulation, 16° 5′ S, 145° 29′ E (QM J36323, J36326–29, J41322, J52165); Charappa Creek, Walter Hill Range, 17° 42′ 20″ S, 145° 40′ 20″ E (QM J66040–42, J67192); Charmillan Creek, Tully Falls Rd, 17° 42′ S, 145° 31′ E (QM J56144, J56492); Crystal Cascades, 16° 58′ 0″ S, 145° 40′ 40″ E (AMS R55967, QM J62086); Dalrymple Gap,18° 24′ 45″ S, 146° 4′ 58″ E (QM J86782–83); Davies Creek, Kuranda-Mareeba, 17° 3′ S, 145° 33′ E (QM J56181); Dinner Falls, 10 km SE Herberton, 17° 26′ S, 145° 28′ E (AMS R53954); Dirran Creek, 13 km S Malanda, 17° 28′ S, 145° 33′ E (QM J55572–79, J56108–22, J56127, J56178–80, J56498–99); Gap Creek, Mt Finlay, 15° 48′ 45″ S, 145° 19′ 5″ E (QM J57832); Goolagan Creek, 27 km W Innesfail, 17° 36′ S, 145° 48′ E (AMS R85587); Helenvale, 15° 42′ S, 145° 13′ E (AMS R56702); Henrietta Creek, Palmerston Hwy, 17° 36′ S, 145° 45′ E (QM J25570–71, J36332–37, J41085–94, J54926, J56188–90, J65538, J66039, J66045–49); Home Rule Camp, via Wallaby Creek, 15° 44′ S, 145° 18′ E (QM J24857); Home Rule, 4 km E "The Granites", 15° 45′ 40″ S, 145° 20′ 55″ E (QM J25277); Home Rule, Slaty Creek, 15° 44′ S, 145° 18′ E (AMS R26778–79); Home Rule, Wallaby Creek, 15° 44′ S, 145° 15′ E (QM J25147–50, J25180, J25219); Home Rule Falls, 15° 44′ S, 145° 18′ E (QM J25261–62, J75830); 34 km W Innisfail, 17° 34′ S, 145° 45′ E (QM J29717–24); Jira Cave, Russell River, 5.8 km SW Mt. Bartle Frere, 17° 26′ 39″ S, 145° 47′ 10″ E (QM J74726–29); Koombooloomba Dam, 17° 50′ S, 145° 36′ E (QM J29559–62, J29573–75); Little Forks, via Shiptons Flat, 15° 49′ S, 145° 13′ E (QM J27151, J27163, J27259); Maalan State Forest, via Millaa Millaa, 17° 37′ S, 145° 38′ E (QM J31181); Malanda Creek, near Malanda Falls, 17° 21′ S, 145° 36′ E (QM J55844–45); McDowall Range, 16° 6′ 45″ S, 145° 20′ 50″ E (QM J66035–36); McHugh Bridge, 42.8 km E Ravenshoe, 17° 34′ S, 145° 41′ E (QM J29600, J29670–76); Meunga Creek, Cardwell, 18° 16′ 30″ S, 145° 52′ 30″ E (QM J48320–21); Millaa Millaa Falls, 17° 31′ S, 145° 37′ E (QM J55608–15, J56123–26); Millstream National Park, 17° 38′ 35″ S, 145° 27′ 25″ E (QM J67198); Mossman Gorge, 16° 28′ 15″ S, 145° 19′ 40″ E (AMS R26603–05, QM J52164, J52167, J60942); Mt Fox State Forest, 18° 34′ 48″ S, 145° 47′ 1″ E (QM J66044); Mt Hypipamee National Park, 17° 25′ 40″ S, 145° 29′ 15″ E (QM J24529–30, J66108, J66127–28); Mt Lewis, 16° 35′ S, 145° 15′ E (QM J43618); Mt Spec, 18° 57′ S, 146° 11′ E (QM J36309–11, J36318–20, J41084); Mt Spurgeon, 16° 26′ S, 145° 12′ E (QM J56186–87, J56700); northern Queensland (QM J41321); O'Keefe Creek, Big Tableland, 15° 42′ 30″ S, 145° 16′ 30″ E (QM J63708–09); Palmerston, 17° 37′ S, 145° 40′ E (QM J32066–67); Palmerston Hwy, 17° 34′ S, 145° 42′ E (QM J31966); Palmerston Hwy, near Millaa Millaa, 17° 34′ S, 145° 42′ E (QM J32080, J32098, J32131–32, J32139); Palmerston National Park, 17° 35′ 58″ S, 145° 45′ 27″ E (AMS R33423, QM J63702); Palmerston National Park, Boulder Creek, 17° 37′ S, 145° 40′ E (QM J36314–17, J36338–47); Palmerston Rocks National Park, 17° 34′ 30″ S, 145° 53′ 30″ E (QM J61320, J87114); Paluma, 19° 0′ S, 146° 12′ E (QM J29593–96, J30899, J32097, J32122, J32173); Parrot Creek, Shiptons Flat, 15° 48′ S, 145° 16′ E (QM J13158, J40547); South Johnston River, near Millaa Millaa, 17° 40′ S, 145° 48′ E (QM J56139–43); Stallions Pocket, Mulgrave River, 17° 12′ S, 145° 45′ E (QM J30905–06, J30908–12, J32068, J32091, J32096, J32101–02, J32130, J32166, J32168); The Boulders, Babinda, 17° 20′ S, 145° 54′ E (QM J36330–31, J41076–78, J41081–83); The Crater, 17° 26′ S, 145° 29′ E (QM J30700, J30917–19, J32095); Thiaki Rd, 6 km E Mt Hypipamee National Park, 17° 25′ S, 145° 32′ E (QM J32164–65); Tully, 17° 46′ 30″ S, 145° 38′ 30″ E (QM J60922); Tully Falls, 17° 46′ S, 145° 34′ E (QM J29258, J32065, J32092, J32100, J32169, J32174, J36308, J36312–13, J36321–22, J41079–80, J56161–70); Tully River, H Rd, 1 km from Tully River bridge, 17° 46′ 45″ S, 145° 39′ 40″ E (QM J48195–98); Tully River, 1st Creek E of bridge, 17° 47′ 30″ S, 145° 40′ 30″ E (QM J60950); Tully River, 2nd Creek E of bridge, 17° 48′ 30″ S, 145° 41′ 30″ E (QM J60913, J60948); Upper Russell River, W slope Mount Bartle Frere, 17° 23′ S, 145° 42′ E (AMS R61388, QM J56148–49); Wallaman Falls National Park, 18° 34′ 30″ S, 145° 47′ 30″ E (QM J61292–93, J61299–300); Walsh Falls, 3 km from Atherton, 17° 18′ S, 145° 25′ E (QM J56150–53); West Mulgrave River, W side Mt Bellenden Ker, 17° 17′ S, 145° 48′ E (QM J56128–38, J56154–60, J56171–77, J56495); Windsor Tableland State Forest, 16° 12′ 30″ S, 144° 58′ 30″ E (QM J52166, J57847); Wongabel area, 17° 19′ S, 145° 26′ E (QM J43684–87); Yuccabine Creek, Kirrama State Forest, 18° 12′ 30″ S, 145° 45′ 50″ E (QM J71258).

RESULTS

Most specimens examined had the pupil so widely dilated that it appeared either round or diamond-shaped, with neither axis unambiguously narrower than the other. Many of these also had a white flocculant material beneath the cornea that made determining the pupil's outline difficult. Nonetheless, in several dozen specimens with clearly viewable, nicely contracted pupils, these were invariably oriented with the long axis on the horizontal plane, as seen in any other *Litoria* species. AMS 26604, 39722, and 61388 serve as exemplars illustrating this character state. No specimen had the vertical pupil characteristic of *Nyctimystes* and observed by me in hundreds of specimens of more than 20 species in that genus (partial list provided in Kraus (2012)).

DISCUSSION

The significance of a horizontal pupil in *Litoria dayi* is that previous assignment of these frogs to the genus *Nyctimystes* was in error, being based solely on possession of a palpebral reticulum, a feature that comprises only one of the two characters that *in combination* define the genus and which was first used to assist in diagnosing the genus more than 40 years after it was defined on the basis of pupil shape. How is it that the failure of *Litoria dayi* to meet both morphological criteria for valid membership in *Nyctimystes* could be overlooked for approximately 50 years? Tyler (1964) first placed his *N. hosmeri* and *N. vestigea* in *Nyctimystes* based on their possessing the characteristic palpebral reticulum of that genus. However, both species were described from single specimens, each of which had a widely dilated pupil whose orientation could not be distinguished as either vertical or horizontal; hence, the second diagnostic character for membership in the genus could not be assessed. Similarly, Tyler (1968) transferred *Hyla tympanocryptis* to *Nyctimystes* on the basis of examining the holotype (and sole known specimen) but without noting the character state for the pupil, a point on which Andersson (1916) was also silent. Liem (1974) used adult body size, extent of finger webbing, and dorsal color pattern in determining that *Hyla dayi* should be referred to *Nyctimystes*; he also made no mention of pupil shape in his specimens. More problematically, Czechura *et al.* (1987) stated in their summary description of *N. dayi* "Pupil vertically elliptical". But, even though they examined a large series of specimens, their claim is directly contradicted by my observations of the same material (Appendix I). Hence, it would appear to be not an empirical assessment of the character so much as a pro forma statement of expectation based on judging that the species belonged in *Nyctimystes* given its obvious palpebral reticulum. The similar claim for a vertical pupil in Cogger (1975) should also be viewed as non-empirical inasmuch as that is a secondary literature source. Thus, the origin of this easily observed error and its persistence for almost 50 years likely derives from original allocation of these frogs to *Nyctimystes* solely based on presence of the palpebral reticulum, correlation of that feature with a vertical pupil in other Australo-Papuan hylids, assumption that this correlation applied as well in Australian frogs having a palpebral membrane, and failure of subsequent researchers to critically evaluate prior literature claims. Interestingly, Davies and Richards (1990, fig. 3) illustrated a horizontal pupil in the tadpole of *L. dayi* but did not remark upon the feature.

The discovery that *Hyla dayi* and its synonyms do not fit with *Nyctimystes* on morphological grounds conforms with recent molecular evidence indicating that the species rightly belongs in *Litoria* and not with *Nyctimystes* (e.g. Frost *et al.* 2006; Rossauer *et al.* 2009; Faivovich *et al.* 2010; Wiens *et al.* 2010). Indeed, *L. dayi* appears closely related to the same species group (*L. nannotis*, *L. nyakalensis*, *L. rheocola*) from which Liem (1974) originally distinguished it (Rossauer *et al.* 2009). That a palpebral reticulum could evolve multiple independent times within Pelodryadinae is unsurprising, given that it has clearly done so as well in two distantly related American hylid genera as well as in unrelated rhacophorid treefrogs. In this regard, it is worth noting that some other *Litoria* have pigmented

patterns on the palpebrum (e.g., *Litoria sauroni* [Richards & Oliver, 2006] and an undescribed *Litoria* in possession of the author), although these do not form a reticulum, so *Litoria* is clearly more variable in palpebral pigmentation than earlier thought. Future study of fresh material of the Halmaheran *N. rueppelli* (Boettger, 1895) may show that species to provide another such instance inasmuch as it too was assigned to *Nyctimystes* solely on the basis of presence of a palpebral reticulum and it represents the only species assigned to *Nyctimystes* having a darkened animal pole to the eggs (Zweifel 1958); hence, it may also prove to be unrelated to the Papuan species that otherwise comprise the genus.

That placement of *Hyla dayi* in *Nyctimystes* was not justified morphologically might seem a trivial discovery except that it impacts on recent interpretations of the monophyly of *Nyctimystes*. In their large study of lissamphibian phylogeny, Frost *et al.* (2006) included ten species as exemplars of pelodryadine hylid frogs, including two putative members of *Nyctimystes*: "*N.*" *dayi* and *N. pulcher*. They found the latter two species to not group together, concluded on that basis that *Nyctimystes* was paraphyletic, and accordingly synonymised that genus with *Litoria*. Doing this created a *Litoria* with 197 species that is synonymous with the already recognised presumptive clade Pelodryadinae (Tyler 1971; Savage 1973). Frost *et al.* (2006) expressed some surprise at their finding of paraphyly in *Nyctimystes*, noting that "morphological evidence would suggest that *Nyctimystes* is monophyletic". That conundrum is readily explained, however, when one recognises that *Hyla dayi* was improperly assigned to *Nyctimystes* to begin with and that, accordingly, Frost *et al.* (2006) did not actually provide a test of the monophyly of *Nyctimystes*.

Subsequent to Frost *et al.* (2006), more comprehensive molecular-phylogenetic surveys of pelodryadine hylids have (depending on the study) included 6–12 Papuan exemplars of *Nyctimystes* and consistently recovered that genus as monophyletic (Rossauer *et al.*, 2009; Faivovich *et al.*, 2010; Wiens *et al.*, 2010). These findings, coupled with recognition that *L. dayi* was improperly included in *Nyctimystes*, support taxonomic revalidation of *Nyctimystes* as a clade of distinctive Papuan stream-breeding frogs. Of course, recognising *Nyctimystes* as a valid clade once again leaves *Litoria* paraphyletic, pending additional resolution of relationships within Pelodryadinae and taxonomic action on those findings. However, that unsatisfactory situation has long been recognised anyway, at least by implication (e.g. Tyler & Davies 1979; Hutchinson & Maxson 1987), is merely provisional until a well-supported monophyletic taxonomy is available for the group, and has the advantage of meanwhile identifying two clades (Pelodryadinae, *Nyctimystes*) instead of the single clade (*Litoria* = Pelodryadinae) proposed by Frost *et al.* (2006). Since identifying and taxonomically recognising distinctive clades is a major goal of modern systematics, reinstatement of *Nyctimystes* as a valid genus meets this goal better than the current pelodryadine taxonomy (Frost *et al.* 2006; Frost 2012).

Lastly, removal of *Litoria dayi* from association with *Nyctimystes* suggests an additional morphological feature that may add to the diagnosis of *Nyctimystes*. All eight species of *Nyctimystes* osteologically examined in detail by Tyler & Davies (1979) have the pars facialis of the maxilla well developed and (in all but one species) in contact with the maxillary process of the nasal. In *Litoria*, the pars facialis varies from shallow to deep but is not in contact with the nasal, except in the *L. aurea* group (Tyler & Davies 1978, 1979). Should this finding be confirmed across a broader taxonomic sample of pelodryadine frogs and should nasal-maxilla contact prove derived within pelodryadines, it would provide further support for monophyly of *Nyctimystes*.

ACKNOWLEDGEMENTS

I thank Patrick Couper and Andrew Amey for graciously hosting my research at QM, Ross Sadlier and Cecilie Beatson for doing the same at AMS, and Glenn Shea for comments on an earlier draft of the manuscript and for notifying me about the illustration in Davies and Richards (1990). This research was supported by National

Science Foundation grants DEB-0743890 and DEB-0103794. This is contribution 2012-013 from the Pacific Biological Survey at the Bishop Museum.

LITERATURE CITED

Andersson, L.G. 1916. Results of Dr. E. Mjöbergs Swedish scientific expeditions to Australia 1910–1913. IX. Batrachians from Queensland. *Könglige Svenska Vetenskaps-Akademiens Handlingar* (new series) **52**(9): 1–20.

Boettger, O. 1895. Liste der Reptilien und Batrachier der Insel Halmaheira nach den Sammlungen Prof. Dr. W. Kükenthal's. *Zoologischer Anzeiger* **18**: 129–138.

Boulenger, G.A. 1914. An annotated list of the batrachians and reptiles collected by the British Ornithologists' Union Expedition and the Wollaston Expedition in Dutch New Guinea. *Transactions of the Zoological Society of London* **20**: 247–274.

1897. Descriptions of new lizards and frogs from Mount Victoria, Owen Stanley Range, New Guinea, collected by Mr. A. S. Anthony. *Annals and Magazine of Natural History*, 6th series **19**: 6–13.

1882. *Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum*, 2nd ed. (Taylor & Francis: London).

Cogger, H.G. 1975. *Reptiles and amphibians of Australia*. (Ralph Curtis Books: Hollywood, Florida, USA).

Copland, S.J. 1957. Australian tree frogs of the genus *Hyla*. *Proceedings of the Linnean Society of New South Wales* **83**: 9–108.

Czechura, G.V., Ingram, G.J. & Liem, D.S. 1987. The Genus *Nyctimystes* (Anura: Hylidae) in Australia. *Records of the Australian Museum* **39**: 333–338.

Davies, M., & Richards, S.J. 1990. Developmental biology of the Australian hylid frog *Nyctimystes dayi*. *Transactions of the Royal Society of South Australia* **114**: 207–211.

Faivovich, J., Haddad, C.F.B., Baêta, D., Jungferd, K.-H., Álvares, G.F.R., Brandão, R.A., Sheil, C., Barrientos, L.S., Barrio-Amorós, C.L., Cruz, C.A.G. & Wheeler, W.C. 2010. The phylogenetic relationships of the charismatic poster frogs, Phyllomedusinae (Anura, Hylidae). *Cladistics* **26**: 227–261.

Frost, D.R. 2012. Amphibian species of the world: an online reference, version 5.5. Available at http://research.amnh.org/vz/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA.

Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B.,de Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M. & Wheeler, W.C. 2006. The amphibian tree of life. *Bulletin of the American Museum of Natural History* **297**: 1–370.

Günther, A. 1897. Descriptions of new species of lizards and of a tree-frog from north-eastern Queensland. *Novitates Zoologicae* **4**: 403–406.

Hutchinson, M.N. & Maxson, L.R. 1987. Phylogenetic relationships among Australian treefrogs (Anura: Hylidae: Pelodryadinae): an immunological approach. *Australian Journal of Zoology* **35**: 61–74.

Kraus, F. 2012. A new species of *Nyctimystes* (Anura: Hylidae) from Papua New Guinea. *Herpetologica*. **68**: 541-550

Liem, D.S. 1974. A review of the *Litoria nannotis* species group, and a description of a new species of *Litoria* from northern Queensland, Australia (Anura: Hylidae). *Memoirs of the Queensland Museum* **17**: 151–168.

Loveridge, A. 1935. Australian amphibia in the Museum of Comparative Zoology, Cambridge, Massachusetts. *Bulletin of the Museum of Comparative Zoology, Harvard* **78**: 1–62.

Parker, H.W. 1936. A collection of reptiles and amphibians from the mountains of British New Guinea. *Annals and Magazine of Natural History*, 10th series **17**: 66–93.

Richards, S.J. & Oliver, P.M. 2006. Two new species of large green canopy-dwelling frogs (Anura: Hylidae: *Litoria*) from Papua New Guinea. *Zootaxa* **1295**: 41–60.

Rossauer, D., Laffan, S.W., Crisp, M.D., Donnellan, S.C. & Cook, L.G. 2009. Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology* **18**: 4061–4072.

Savage, J.M. 1973. The geographic distribution of frogs: patterns and predictions. Pp. 351–445. *In* Vial, J.L. (ed.) *Evolutionary biology of the anurans: contemporary research on major problems*. (University of Missouri Press: Columbia).

Stejneger, L. 1916. New generic name for a tree-toad from New Guinea. *Proceedings of the Biological Society of Washington* **29**: 85.

Tyler, M.J. 1971. The phylogenetic significance of vocal sac structure in hylid frogs. *University of Kansas Museum of Natural History Occasional Papers* **19**: 319–360.

1968. An additional species of the hylid frog genus *Nyctimystes* with notes on *Hyla dayi* Gunther. *Arkiv för Zoologi* **20**(22): 501–504.

1964. Two new species of Australian frogs of the hylid genus *Nyctimystes*. *Transactions of the Royal Society of South Australia*. **88**: 111–114.

Tyler, M.J & Davies, M. 1979. Redefinition and evolutionary origin of the Australopapuan hylid frog genus *Nyctimystes* Stejneger. *Australian Journal of Zoology* **27**: 755–772.

1978. Species-groups within the Australopapuan hylid frog genus *Litoria* Tschudi. *Australian Journal of Zoology, Supplementary Series* **63**: 1–47.

Wiens, J.J., Kuczynski, C.A., Hua, X. & Moen, D.S. 2010. An expanded phylogeny of treefrogs (Hylidae) based on nuclear and mitochondrial sequence data. *Molecular Phylogenetics and Evolution* **55**: 871–882.

Zweifel, R.G. 1958. Results of the Archbold Expeditions. No. 78. Frogs of the Papuan hylid genus *Nyctimystes*. *American Museum Novitates* **1896**: 1–51.